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HABITATS OF LARVAL TABANIDAE (DIPTERA) IN SOUTH TEXAS[1]

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Abstract.—Through the use of physical and chemical methods, the habitats and interspecific associations of 12 species of Tabanidae in SE Texas are described. The Navasota River floodplain near College Station was the most prolific source, producing 298 larvae in 28 soil treatments with pyrethroid emulsions applied 29 March–12 August 1976. Five species were represented in the sample population of larvae here: *Tabanus atratus* F., 41.8%; *T. proximus* Walker, 36.8%; *T. subsimilis subsimilis* Bellardi, 14.4%; *T. trimaculatus* Palisot de Beauvois, 5.6%; and *T. lineola* F., 1.4%. This total of five species comprised less than one-fifth of the 26 species taken as adults by Gressitt Traps the previous season (1975); among the 21 species not collected as larvae in 1976 were numerous forms comprising up to 8.3% of the adult sample population. Conversely, the most abundant species represented in larval collections was *T. atratus*, a form including only 0.1% (14 specimens) of the adults collected in 1975. Larvae of one or two species predominated at any given site and time, with only several specimens of a 2nd or 3rd species being found under these conditions. Low indices of affinity suggest that no specific association existed between larvae of any two species found together.

The data on larvae reported here were taken in conjunction with those of adults published for several ecosystems of SE Texas; coastal marshes (Thompson, 1973a); coastal prairies (Thompson, Blume and Aga, 1977); the Pine Belt (Thompson, 1973b, 1974b, 1976); and the Post Oak Belt (Thompson, 1974a, 1976, 1977). Because of the kinds of ecosystems selected and the collecting methods used, these initial studies were not very productive. Then the discovery of larvae of *Tabanus subsimilis subsimilis* Bellardi in varied upland soil situations, and the subsequent successful use of pyrethrin emulsions for collecting this species for rearing purposes (Thompson, 1975), stimulated further application of this insecticide formulation for locating larval populations of Tabanidae. Use of pyrethrins improved productivity—i.e., more larvae were removed from larger areas in less time—and surveys, rather than collections, became the major effort.

During the last two years then, larval populations were sampled in ecosystems which demonstrated large populations of Tabanidae in previous research with adults, which were located near the laboratory and which provided soils where intoxicated larvae could be seen after surfacing. The latter criterion required that surface treatments be made in soils lacking the dense sod of marshes and grasslands or pasture and lawn turfs. Therefore, the forest floors of a river floodplain and an upland wooded ridge some 12 mi away provided the most suitable substrata for application of pyrethrin emulsions. This paper presents data based upon these collections, and others using mechanical methods, from south Texas study areas.

The Study Areas

The physiography and vegetation of the two primary study areas near College Station were described by Thompson (1974a, 1977). Briefly, the upland locality is a ridge of home properties and adjoining woodlots, the latter consisting largely of post oaks (*Quercus stellata* Wang.) on the ridges proper, and water oaks (*Q. nigra* L.) in the gullies and washes. The brushy shrub understory consists mostly of yaupon (*Ilex vomitoria* Ait.) and dense lianas. Some 12 miles away, the Navasota River floodplain forms a 2-mile-wide basin overlain with three natural vegetative cover types: Upland Forest, like that previously described, on the upper slopes and flats; Transition Forest on the basal slopes below; and Bottomland Forest on the floodplain proper. These forests are comprised of woody plant communities, the nine dominant overstory species of which form a continuum, gradually replacing one another from the uplands onto the floodplain, and then to the river margin, and are: post oak, black hickory (*Carya texana* Buckl.), winged elm (*Ulmus alata* Michx.), overcup oak (*Quercus lyrata* Walt.), willow oak (*Q. phellos* L.), cedar elm (*Ulmus crassifolia* Nutt.), water elm (*Planera aquatica* Gmel.), swamp privet (*Forestiera acuminata* (Michx.) Poir.), and black willow (*Salix nigra* L.). The topography of these lowlands is frequently flooded for short periods and occasionally, for weeks or months.

Methods

Initial studies employed a variety of mechanical devices and methods of extraction: A kitchen sieve; a modified Berlese-Tullgren Funnel apparatus; a hand cultivator for garden use; salt flotation; and a "comb" made from a wooden dowel and finishing nails (Thompson, 1970a). In the work reported here, the hemispherical kitchen sieve was replaced by one made from a stainless steel food service tray (12 × 20 × 2.5 in). The floor of the tray was cut out and covered with ¼ in mesh hardware cloth or 16-mesh wire screen—the size depending upon the texture of the soil being processed. This tray-sieve increased the volume and the sieving surface of the soil being examined and was invaluable for processing sands and alluvium in stream beds and in river floodplains. In order to find equipment for processing more soil in less time, several power-driven farm and garden implements were also used. A tractor-driven chisel was used to examine floodplain soils along the Bois d'Arc Creek (where heavy populations of *Tabanus s. subsimilis* were then seriously infesting the Red River watershed). Although no larvae were found as the gang of chisel blades cut and turned the sod to a depth of 1–2 in, the presence of earthworms and white grubs in the furrows or excavated soil showed that if numerous tabanid larvae had been present, some would have been exposed in these examinations. (Under similar circumstances—in plow furrows of cultivated fields—Davis (1919) and his colleagues found larvae of *T. sulcifrons* Macquart in Kansas, Maryland and Mississippi.) In addition to the chisel, a gasoline-driven rotary tiller was used to turn soils previously shown to contain *T. s. subsimilis*, again with negative results.

Two commercial pyrethroid formulations were used as sources of the active ingredient: An oil solution of pyrethrins (Gulfspray, Gulf Oil Corp.) which was emulsified with Triton X-100 (Rohm and Haas Co.) before addition of tap water and an emulsifiable concentrate of resmethrin (Super Syn 30EC, Redmond Chemical, Inc., Houston, Texas). After the removal of organic debris, 0.002% emulsions were applied as drenches to measured areas of soil surface. Where rainfall and evaporation allowed, 1 gal of solution per sq yd was usually sufficient to saturate mineral soils. In most cases, larvae were sought in treated plots for at least 2 h after treatment. Observations, during two treatments yielding 59 and 61 larvae of *T. s. subsimilis* (other details of study were presented by Thompson (1975)), showed that intoxicated larvae can emerge up to 18 h after treatment and that a large percentage of these, one-third to one-half, can be expected to surface after the first hour posttreatment. Several important procedures for posttreatment handling of intoxicated specimens can increase their survivorship for later rearing purposes. During the present study, up to half of those larvae emerging within the first several hours, when first washed with a mild Triton X-100 solution in water and then held in the lab at 20–25°C, were suitable for rearing in the laboratory.

Considering the temperature, pyrethroids are more active at lower temperatures down to 5°C, like DDT, whereas these materials become less effective at temperatures approximating 20–25°C. Toxicological effects, too, become very significant in affecting behavior and survival after treatment. For example, pyrethrins are more effective irritants upon insects than synthetic pyrethroids; on the other hand, synthetic pyrethroids, such as resmethrin, are more potent insecticides. Finally, in addition to their noxious effects upon insects, the dermatogenic and allergenic properties of these chemicals should be seriously considered by those persons using them.

Immatures were maintained in 2 oz clear glass jars, the Bakelite lids of which were center-drilled with 1 in holes and covered by fine-mesh metal screen. The substratum of washed builder's sand was washed with tap water weekly and the tabanid larvae were fed those of house flies and stable flies. A 14½ h photoperiod was provided with a timer-controlled 15 W fluorescent bulb.

Results and Discussion

But for the numerous larvae of *T. s. subsimilis* reported from two grassy seepage areas near domestic septic tanks (Thompson, 1975), and for lesser numbers of this species taken here in several subsequent collections, only one soil treatment in that locality produced larvae of any other species. In Thompson's four treatments totaling 81 sq ft of soil, nine larvae were recovered from the damp and leaf-littered depressions of dry-wash gullies in the adjacent post oak forest; seven of those larvae were *T. s. subsimilis* (instead of one, as previously shown in Thompson's 1975 publication). The two larvae remaining, included one specimen each of *Tabanus atratus* F. and *T. trimaculatus* Palisot de Beauvois. The only species taken by mechanical methods in other collections included one additional specimen of these two species and four specimens of *Leucotabanus annulatus* (Say). The larval habitats of these, and the other species considered here, will be described in a later section.

Lowland Locale

The most productive collections were made with pyrethrins on litter-laden soils beside standing water on the Navasota River floodplain near College Station. Of 28 treatments applied on 18 days from 29 March–12 August 1976, 23 treatments were positive for larvae. These collections yielded 285 specimens of five species and 13 more individuals of undetermined identity. Of the 298 specimens obtained, 1–38 were taken per positive treatment, with an average of 13.

Relative abundance of different species in the larval sample population and of species in the larval and adult sample populations.—In decreasing order of abundance, the five species collected as larvae were *Tabanus atratus*, *T. proximus* Walker, *T. s. subsimilis*, *T. trimaculatus*, and *T. lineola* F. (see Table 1 for numbers). These five tabanid species included only one-fifth of the 26 species taken by Gressitt Traps with CO_2 the year before (Thompson, 1977). Some of these 21 species were abundant or numerous in the adult sample population; i.e., *Tabanus sulcifrons*, *T. fuscicostatus* Hine and *Hybomitra lasiophthalma* (Macquart) comprised 8.3, 5.3 and 4.5% of that catch, respectively. On the other hand, *Tabanus proximus*, *T. s. subsimilis* and *T. lineola*, the three other species included among the six most abundant species taken as adults in 1975, were easily observed in larval collections in 1976 (Table 2). More significantly, the most abundant species represented in larval collections was *T. atratus*, a form including only 0.1% of the adults collected in 1975.

Similar results to those above, based upon adult and larval collections

Table 1. Larval samples of five species of *Tabanus* collected by pyrethroid treatments of soils on a Navasota River floodplain forest, Brazos Co., Texas, 29 March–12 August 1976 (positive treatments and identified specimens only).

Date	*atratus*	*proximus*	*subsimilis*	*trimaculatus*	*lineola*	Total
Mar. 29	3		4			7
Apr. 1	14	3				17
2			2			2
9	7	2				9
19	3	3				6
19	1	6	2	(1)[a]		10
19	8		2	1		11
May 24				1		1
24		27		2		29
24		18				18
25		3	6	4	2	15
25	1	5		1	1	8
Jun. 11		10				10
14		11		1		12
18		10	2			12
23		7				7
Aug. 2	13		2	4		19
3	8		14		1	23
4	19			2		21
4			3			3
4	7					7
9	35		3			38
12			1			1
Totals	119	105	41	16	4	285
Incidence[b]	52%	52%	48%	3%	13%	

[a] This figure represents one pupa of this species and is not included in the total of larvae below, or in any other total presented in this paper.

[b] The percentage of 23 positive collections producing the species.

in two other Coastal Plain study areas, are presented in Tables 3 and 4. Larval collections produced approximately one-quarter, or less, of the 40 species taken as adults in each study area. Based on data from the work at both the Great Swamp National Wildlife Refuge (Thompson, 1967, 1970a) and the Patuxent Wildlife Research Center (Thompson, 1970b, 1971), ranking of species demonstrated little correlation between larval and adult sample populations (Tables 3 and 4).

Larval sample populations in these ecosystems included one or two of the most abundant dominants and ignored the presence of the others. On the other hand, the one most abundant species of larva at Great Swamp and Patuxent was much less numerous in adult collections: *Tabanus marginalis* F. included less than 1% of the adult sample population (as for *T.*

Table 2. Comparison of larval sample population, Navasota River floodplain, 1976 season, with that of adults of Tabanidae from the same locale, 1975 season.[a]

	Larvae			Adults		
	Rank	%	(number)	Rank	%	(number)
Tabanus						
atratus	1	41.8	(119)	18	0.1	(14)
proximus	2	36.8	(105)	2	12.8	(1,648)
subsimilis	3	14.4	(41)	1	55.9	(7,172)
trimaculatus	4	5.6	(16)	8	2.0	(256)
lineola	5	1.4	(4)	3	4.3	(555)
21 spp. left		0	(0)		24.9	(3,195)
Totals		100	(285)		100	(12,840)

[a] Rank of adults is based upon a total of 26 species collected.

atratus at the Navasota River); and specimens representing either one or both of *T. melanocerus* Wiedemann and *T. petiolatus* Hine (the two are presently inseparable in the larval stage) dominated larval collections in a population where the adults were only commonly collected, rather than very numerous.

Density.—From 1–8 sq yds of soil surface (total = 81) were treated in those applications producing larvae. Densities ranged from 0.4–14.5 larvae per sq yd, with an average of 3.7. There was no correlation between density and the presence of standing water or the presence of leaf litter, the time of collection, the identity of the species collected, or the number of species associated together.

Interspecific association.—As mentioned previously, the most numerous species in larval collections were also the most frequent species taken

Table 3. Comparison of larval and adult sample populations of Tabanidae, Great Swamp National Wildlife Refuge, Morris Co., New Jersey 1966–1967.[a,b]

	Larvae			Adults		
	Rank	%	(number)	Rank	%	(number)
T. marginalis F.	1	80.8	(184)	17	0.3	(20)
C. vittatus Wied.	2	13.1	(30)	2	21.6	(1,394)
T. lineola F.	3	3.5	(8)	1	24.4	(1,573)
C. univittatus Macq.	4	2.6	(6)	14	0.7	(50)
36 spp. left		0	(0)		53.0	(3,434)
Totals		100	(228)		100	(6,471)

[a] Rank of adults is based upon a total of 40 species collected.

[b] Several specimens of undetermined species of *Atylotus* and *Hybomitra* are not included here.

Table 4. Comparison of larval and adult sample populations of Tabanidae, Patuxent Wildlife Research Center, Prince Georges Co., Maryland, 1968–1969.[a]

	Larvae			Adults		
	Rank	%	(number)	Rank	%	(number)
T. melanocerus Wied.;	1	44.7	(120)	14	0.7	(35)
T. petiolatus Hine[b]	—	—	—	11	4.4	(203)
C. vittatus Wied.	2	25.7	(69)	1	13.8	(648)
T. trimaculatus Palisot de Beauvois	3	18.6	(50)	8	6.3	(292)
T. lineola F.	4	3.0	(8)	9	5.6	(259)
T. sulcifrons Macq.	5	2.7	(7)	13	1.3	(64)
T. nigripes Wied.	6	2.2	(6)	23	0.1	(6)
T. marginalis F.	7	1.4	(4)	23	0.1	(6)
T. similis Macq.	8	0.7	(2)	32	>0.1	(1)
C. carbonarius Walk.	8	0.7	(2)	36	>0.1	(3)
C. dimmocki Hine	9	0.3	(1)	36	>0.1	(3)
29 spp. left		0	(0)		67.7	(3,181)
Totals		100	(269)		100	(4,701)

[a] Rank of adults is based upon a total of 40 species collected.
[b] These two species are indistinguishable in the larval stage.

then. Yet the incidence of more than two species together in any given treatment was low (6 of 23 collections or 26%). Furthermore, the use of Fager's Index of Affinity for these treatments illustrates the low frequency with which any 2 species were found together. This index equals twice the number of joint occurrences divided by the total occurrences of both species taken in all samples. Through the use of a table providing the minimum values of joint occurrence which are significant at the 0.5 level (Fager, 1957), it is possible to recognize quickly pairs of species which are decidedly associated versus those which show no evidence of affinity at all. At some later time then, additional and more specialized sampling techniques can be used to study those associations which are questionable.

With the exception of *T. lineola*, which was inadequately represented in the sampling reported here, Fager's Indices for each association are shown in Table 5; testing these indices with the table provided by Fager, no significant association was found between any two of the other four species considered here. Therefore, collection of any one of these species did not increase the chance of finding any other species associated with it.

The low Indices of Affinity found here support the idea that these tabanid species of the predominantly cannibalistic genus *Tabanus* compete fiercely for space in mutually satisfactory habitats. Also, these low Indices for the large *T. atratus* and *T. proximus* species could result more from their dominant size than from their absolute abundance (as indicated by their

Table 5. Fager's Indices of Affinity for five species of *Tabanus* associated together, Navasota River floodplain, Brazos Co., Texas, 29 March–12 August 1976.

	atratus	*proximus*	*subsimilis*	*trimaculatus*	*lineola*[a]
atratus	—	0.417	0.522	0.400	—
proximus	0.417	—	0.261	0.400	—
subsimilis	0.522	0.261	—	0.316	—
trimaculatus	0.400	0.400	0.316	—	—
lineola[a]	—	—	—	—	—

[a] This species was inadequately represented for assignment of an index.

related abundance in samples of adult insects—*T. proximus*) or their habitat specificity (both species).

Seasonal incidence.—Moving down through the chronologically-ordered list of treatments in Table 1, no striking seasonal differences are apparent in the incidence of any particular species. But for *T. trimaculatus* and *T. lineola*, the least numerous and least frequent species observed, larvae were found throughout the entire period of collection—from spring through summer. With rare exception, larvae of all species were no less than half an inch long. Although no measurements of larval lengths were made, the majority of specimens of each species taken in any given collection were similar in size; this was especially noticeable for the large species, *T. atratus* and *T. proximus*.

The Habitats

The larval stages of 12 species of Tabanidae were obtained by means of pyrethroid treatments in upland and lowland locales near College Station and by mechanical means from these and other study areas in SE Texas.

Chlorotabanus crepuscularis (Bequaert).—One larva was taken from the marginal mud of a slough at the Navasota River Bottoms (NRB), 14 September 1971. Adults of this species were rare from this and the other locales considered here.

Leucotabanus annulatus (Say).—Large larvae of this species were found in their typical habitat, rotting deadfall (4 specimens, Upland Locale, February–May collections; 1 specimen, Huntsville State Park, Walker Co., 19 June 1972).

Tabanus atratus F.—One of the most common species found; one specimen was removed from the grassy septic tank seepage area described by Thompson (1975), where it was associated with 4 larvae of *T. subsimilis subsimilis* (8 June 1976). Some 35 yds away, another larva was found at the margin of a small, shallow pond of some 500 sq ft of surface, which was choked with pickerelweed (*Pontederia*) and duckweed (*Lemna*) (17 April 1974). Also, on a ridge near this site, Christopher Thompson found a larva crawling on the soil surface—a larva which had apparently been disturbed by his deep excavations several feet away (21 March 1976). Larvae were found in shoreline situations near other standing waters (drainage ditch through a coastal marsh which was described by Thompson (1973b), 12 July 1971; and a pond on a municipal golf course, College Station, 1 April 1974). The most prolific sources were the margins of woodland pools and sloughs at NRB; four larvae were found here (in the months of January, February, June and August) before the insecticide treatments later produced 119 specimens (Table 1). Of the latter samples, 116 specimens were found in samples near standing water; the three specimens remaining were removed from a leaf-littered wash.

Tabanus cymatophorus Osten Sacken.—One larva of this large, brightly-marked fly, was taken from the marginal mud of a woodland pond at NRB. Associated with several *T. proximus* larvae nearby in this March collection, the larva was reared to the adult form (female) for determination. The incidence of *T. cymatophorus* as an immature was low compared with the commonness of the adults in 1975 (106 females, late June–early August; Thompson, 1977).

Tabanus lineola F.—This species was found in three NRB collections made with pyrethrin emulsions (Table 1).

Tabanus molestus Say.—One specimen, identified as a larva, was removed from the shoreline of a slough at NRB, 14 September 1971. Adults were not common in previous collections (30 specimens, mid-May to mid-July).

Tabanus petiolatus Hine.—Five larvae were taken from a sandy wash across a firelane in a pine-hardwood forest, Huntsville State Park in September; later in October, three larvae were found in a sandy creek bank of the same forest. Although three of these eight specimens were reared for identification, the closely related *T. melanocerus* is presently unknown from this study area. Lastly, one larva was taken with *T. trimaculatus* and three other species (see *T. trimaculatus*) from the Navasota River. It was later reared for identification.

Tabanus proximus Walker.—The most common form collected from NRB before the 1976 collections using pyrethroids; six collections in March and one in October produced 24 specimens from the margins of ponds and pools. As in later collections with pyrethroids, *T. proximus* was associated with *T. trimaculatus* and *T. atratus*.

Tabanus subsimilis subsimilis Bellardi.—Since the 1975 report, four additional collections of *T. s. subsimilis* were made in the same habitats described then: 1 pupa, in a flower bed skirting a patio and 8 larvae in a grassy alga-covered seepage area (May and June of 1976). In two June collections, one larva was found at the margin of a grassy pasture pond, surrounded by very dense willow saplings, and one larva was removed from the bank of the Navasota.

Tabanus sulicifrons Macquart.—Two specimens, identified as larvae, were taken from the marginal mud of a drainage ditch through a brackish coastal marsh near Angleton in July (habitat described in Thompson, 1973a) and from a pile of dry and duff-like manure in the corner of a hay shed near College Station in September. (Three pupal exuviae, believed to represent a sibling species, were found several inches above the bottom of a dry-wash gully in association with three pupal exuviae of *T. proximus.*)

Tabanus trimaculatus Palisot de Beauvois.—This species was represented in collections from all major locales studied: In a grassy seepage area (1 specimen) together with large numbers of *T. s. subsimilis* (Thompson, 1975); at the margin of a 2-acre impoundment with *Ludwigia* submerged along the littoral zone nearby and smartweed (*Polygonum*) at the shoreline above it (1 larva); in the sandy-creek bed of a pine-hardwood forest, the site previously described for *Tabanus petiolatus*, but on a different occasion (2 larvae); as the predominating species in marginal mud of NRB sloughs in association with *Chlorotabanus crepuscularis, Tabanus atratus, T. molestus* and *T. petiolatus* (7 specimens); at this slough and at woodland pools nearby in March of the following year, in association with 11 specimens of *T. proximus* and 1 of *T. atratus* (7 specimens); and dominating the latter species here the next October (17 specimens to 4 of *T. atratus*); and finally, again in March of the following year, from a woodland pond margin here, where 1 specimen was a small minority among the 13 *T. proximus* specimens found.

Tabanus venustus Osten Sacken.—One specimen, later reared to the adult form (female), was found in March at the margin of a small pond near the College Station municipal airport.

Conclusions

If the adults of Coastal Plain Tabanidae are ubiquitously obvious to the observer, the larvae are patently obscure. Paradoxically, this situation is occasionally reversed, with larval numbers in samples greatly exceeding those of adults: *Tabanus reinwardtii* Wiedemann (Cameron, 1926; Philip, 1931; Schwardt, 1936; Stone, 1930; and Pechuman, 1972); *T. marginalis* (Philip, 1931; Teskey, 1969; and Thompson, 1970a (q.v., Table 3)); *Merycomyia brunnea* Stone (Jones and Anthony, 1964); and *Merycomyia whitneyi* (Johnson) (Pechuman, 1964; Goodwin, 1973; and Philip, Weems, and Fairchild, 1973). In either case of adult or larval preponderance, this disparity between numbers of the two forms has complicated population estimation and retarded understanding of larval ecology.

Comprehension of tabanid larval ecology has also been obscured by the relative ease of finding larvae in marginal habitats, by the relative difficulty of finding them in deeper soils in habitats where they have been previously established and by the consequent understandable biases of scientists focusing their attentions on marginal niches and surficial soils.

This information, based upon accumulated field experience, has been reenforced by several notions originated and perpetuated in the literature—notions categorizing the immatures of Tabanidae, collectively, as aquatic or semiaquatic insects, rather than as soil insects; as specialized forms in choice of habitat niches, instead of as generalized ones; and as air-breathing insects, rather than as those depending very largely upon cutaneous respiration.

Thus biased collecting and published misconceptions regarding the larvae of the family have led to arbitrary classification of groups of species according to habitat. Usage of such terms as aquatic, littoral, submerged and terrestrial have been applied to certain species rather than to the habitats where those species were observed in specific instances. (The larvae of the so-called terrestrial species have been so described because they were found away from habitats near any accumulations of free water. Although some Tabanidae are obviously adapted morphologically for aquatic existence and others are commonly found submerged, proximity to free water probably has little causal relationship in habitat selection for most species of the Atlantic Coastal Plain of North America.)

In conclusion, the cumulative effect of this experience and these ideas in North American research has been to encourage the search for habitats which are as distinctive as the species inhabiting them and to discourage recognition and study of the critical factors limiting the distribution of tabanid larvae in general. For it is the general body of knowledge about larval habitat selection—the critical environmental characteristics many species of Tabanidae hold common—that reveals most about the biology of most of these species as individuals. To wit, the life of the generalized larval type is unknown. The large body of published larval collection data for Coastal Plain species, the most obvious habitat descriptions of which have been conveniently summarized in tabular form for 109 species and subspecies by Goodwin (1967), documents the generalized and nonspecific nature of this habitat selection.

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Footnote

[1] This paper reports the results of research only. Mention of a pesticide in this paper does not constitute a recommendation for use by the U.S. Department of Agriculture nor does it imply registration under FIFRA as amended.